

Chapter 11: Global warming and cyanobacterial harmful algal blooms

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Abstract

The Earth and the oceans have warmed significantly over the past four decades, providing evidence that the Earth is undergoing long-term climate change. Increasing temperatures and changing rainfall patterns have been documented. Cyanobacteria have a long evolutionary history, with their first occurrence dating back at least 2.7 billion years ago. Cyanobacteria often dominated the oceans after past mass extinction events. They evolved under anoxic conditions and are well adapted to environmental stress including exposure to UV, high solar radiation and temperatures, scarce and abundant nutrients. These environmental conditions favor the dominance of cyanobacteria in many aquatic habitats, from freshwater to marine ecosystems. A few studies have examined the ecological consequences of global warming on cyanobacteria and other phytoplankton over the past decades in freshwater, estuarine, and marine environments, with varying results. The responses of cyanobacteria to changing environmental patterns associated with global climate change are important subjects for future research. Results of this research will have ecological and biogeochemical significance as well as management implications.

Introduction

Global warming

The Intergovernmental Panel on Climate Change published its third assessment report in 2001 (IPCC 2001). The report concluded that the Earth is warming, which is causing regional climate changes and influencing many physical, biological and chemical processes (Walther et al. 2002, Treydte et al. 2006). The global average surface temperature increased by $0.6 \pm 0.2^\circ\text{C}$ during the 20th century, with most of the increase observed over the past four decades (Fig. 1). Instrumental measurements and proxy data show that the rate and duration of warming in the 20th century has been greater than in any of the previous nine centuries, and the 1990s were the warmest decade of the millennium (IPCC 2001). The patterns of warming, which influence trends in temperature and precipitation, are regionally highly variable. This can have striking effects on ecological responses to climate change (Walther et al. 2002). Some of the implications of global change for freshwater ecosystems have been reviewed (Carpenter et al. 1992). Evidence shows a lengthened freeze-free season at many mid- and high-latitudes, the retreat of mountain glaciers in non-polar regions, a decrease in snow cover by about 10%, and a decrease of about two weeks in the annual duration of lake and river ice cover in the Northern Hemisphere (IPCC 2001).

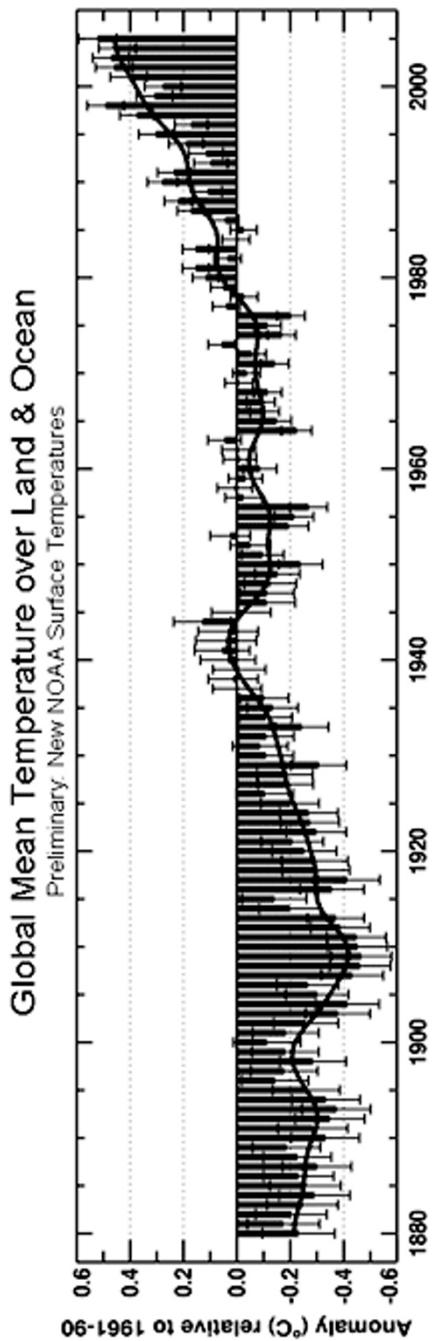


Fig. 1. Time series approximates the temperature of the Earth and how it has been changing through time. Taken from NOAA website. Source: <http://www.ncdc.noaa.gov/img/climate/research/2005/ann/global-blended-temp-pg.gif>

Most of the heating of the earth since the 1950s has occurred in the oceans. During 1955-1998 ocean heat content in the upper 3000 m of the world's oceans increased by 14.5×10^{22} J (a mean temperature increase of 0.037°C) (Levitus et al. 2005). This has led to thermal expansion of the uppermost 700 m layer of the oceans (Antonov et al. 2005), and may lead to greater stratification of the ocean (Hegerl and Bindoff 2005). There is good evidence from modeling studies compared with actual temperature records that atmospheric heat trapped by rising greenhouse gases is responsible for warming the oceans (Barnett et al. 2005). Other impacts of global warming related to sea surface temperature increases may be observed. For example, evidence suggests the destructiveness and number of intense (categories 4 and 5) tropical cyclones has increased over the past 35 years (Emanuel 2005, Webster et al. 2005).

Global climate change also involves stratospheric-ozone depletion, which leads to increased levels of biologically damaging UV-radiation reaching the Earth's surface, and an increasing concentration of atmospheric CO_2 . Increasing CO_2 levels contribute to sea-level rise and alteration of ocean chemistry (Hallock 2005). Changes in ocean chemistry due to increasing atmospheric CO_2 lead to acidification of the ocean (Sabine et al. 2004), which can have profound impacts on calcifying organisms such as corals, calcareous algae, foraminiferans, and mollusks and their rates of calcification (Feely et al. 2004, Hallock 2005).

Evolutionary history of cyanobacteria

Cyanobacteria have been on Earth a very long time-- billions of years. Fossil evidence for the presence of oscillatoreacean cyanobacteria over 3 billion years ago can be found in the 3.5 billion year-old Apex chert deposits in Western Australia (Schopf 2000). Well preserved fossil cyanobacteria are nearly indistinguishable in morphology from their extant relatives and can be found in intertidal and shallow marine environmental settings like those inhabited by cyanobacteria today. Modern cyanobacteria produce 2-methylbacteriohopanepolyols. The geologically stable derivatives, 2α -methylhopanes, serve as biomarkers in sediments for cyanobacteria, which provide further evidence that cyanobacteria were abundant at least 2.5 billion years ago (Summons et al. 1999).

Cyanobacteria can be distinguished from all other prokaryotes by their ability to carry out oxygen-producing photosynthesis. Evidence of both the reactants of oxygenic photosynthesis (H_2O and CO_2) and the products (reduced organic carbon and O_2) can be found in the early rock record of the Apex Chert (Schopf 2000). Although oxygen was being released by

cyanobacteria at least 2.7 billion years ago, a low-O₂ environment is thought to have persisted for at least another 300 million years based on several lines of evidence (Canfield 1999, Kerr 2005). Banded iron formations, iron-oxide rich sediments, are widespread in geologic formations at least 2.5 billion years ago, indicating that molecular oxygen was removed from the system by its reaction with iron during the early Precambrian (Schopf 2000). Sulfur isotope methods applied to rocks of different ages indicate a major change in the sulfur cycle between 2.4 and 2.0 billion years ago (Farquhar et al. 2000), suggesting the appearance of atmospheric oxygen at levels of at least 1 ppm during that time (Kerr 2005). However, it was not until the end of the Proterozoic (600 million years ago) that oxygen rose to near modern levels and multicellular animals appeared (Kerr 2005). The history of the rise of oxygen on the early Earth is the subject of debate among geochemists, paleobiologists and astrobiologists; however, it is clear that cyanobacteria played a significant role in the early evolution of Earth's atmosphere (probably to their own detriment, once multicellular life evolved) (Canfield 1999, Kasting and Siefert 2002, Kerr 2005).

Environmental conditions on the early Earth under which cyanobacteria evolved and thrived were very different from today (Kasting and Siefert 2002). Anoxia, higher UV exposure, higher temperatures, and high levels of iron, sulfide and methane were all factors that influenced early life on Earth. Additionally, cyanobacteria experienced little or no grazing pressure or competition from higher organisms. This may explain why cyanobacteria can thrive under conditions of environmental stress and in extreme environments where they are able to out-compete other organisms. For example, in coral reef habitats cyanobacteria are becoming increasingly dominant on degraded reefs because of their ability to tolerate the environmental conditions associated with anthropogenic impacts and global climate change (Hallock 2005).

Cyanobacteria greatly increased in abundance following mass extinction events (Copper 1994, Hallock 2005). Sheehan and Harris (2004) documented a resurgence of microbialites following the late Ordovician extinction event in western North America approximately 440 million years ago. Microbialites, including stromatolites and other microbial mats that bind sediments, precipitate minerals, and form crusts, increased in size, abundance, and morphological diversity following the late Ordovician extinction event. The period of microbialite resurgence lasted about 5 million years and corresponded with low faunal diversity during the post-extinction recovery period. Similar microbial expansion has been documented after the Permian-Triassic faunal mass extinction (Xie et al. 2005), approximately 250 million years ago, which eliminated over 90% of all marine species (Jin et al. 2000). A survey of microbial biomarkers in

sedimentary rocks in South China spanning the Permian-Triassic (P/TR) boundary was conducted and compared with faunal extinction patterns (Xie et al. 2005). Both cyanobacterial biomarker and invertebrate fossil records showed evidence for two periods of extinction and ecosystem change across the P/Tr boundary. Dramatic changes in the cyanobacterial community followed the two episodes of faunal mass extinction. Two maxima in the 2α -methylhopane (2-MHP) indices following faunal extinctions indicated either a change in the cyanobacterial community (because not all cyanobacteria produce 2-MHPs) or an increase in the abundance of cyanobacteria. Xie et al. (2005) suggested that cyanobacteria dominated following the mass extinction because of low faunal diversity and lack of grazing pressure.

In a review of expansion and collapse of reef ecosystems during the Paleozoic era and examination of reefs existing during periods of less than optimal environmental conditions, Copper (1994) concluded that periodic collapse of reefs and extinction of reef fauna serve as a good indicator of global change. The disappearance of reefs in the geologic record often preceded global mass extinction events by 0.5-1 million years. Copper (1994) termed "disaster species" as groups of organisms that are extinction resistant or ecological opportunists that can survive under marginal conditions. "Disaster species" include cyanobacteria, calcareous algae, encrusting foraminiferans and bryozoans, and these organisms are major components of reef communities during times of reef collapse (Copper 1994). The final remnants of reefs undergoing extinction were covered by skeletal, carbonate-secreting cyanobacteria, and reefs that developed after extinction events featured these and other "disaster species". Environmentally tolerant cyanobacteria, which are resistant to strong solar radiation, higher temperatures, abundant nutrients, and many generalist grazers, may be useful indicators of stress conditions in reef ecosystems today (Hallock 2005).

In this introduction I have set the stage for further discussion of the influence of climate change on cyanobacteria in aquatic and marine habitats. Global climate change is occurring, which is already causing changes in terrestrial and marine ecosystems (Walther et al. 2002). Based on geological records, paleobiological evidence, and physiological and ecological studies, cyanobacteria seem likely to benefit from environmental changes associated with global warming. I review specific physiological and ecological examples below as well as the few studies that have directly examined the effects of climate change on cyanobacterial abundance.

Environmental influences on cyanobacterial growth and toxicity

Chemical defenses

Toxicity in cyanobacteria has been reported since the late 19th century, mostly from poisonings in freshwater environments (Carmichael et al. 1990). These reports describe sickness and death of livestock, pets and wildlife following ingestion of water containing blooms of toxic algae. Cyanobacterial toxins and other bioactive compounds have been the subject of many investigations by toxicologists and natural products chemists (Chorus 2001, Gerwick et al. 2001). These substances are of considerable importance because of their public health implications (Codd et al. 2005) but have also been examined for possible biomedical uses as antitumor compounds (Burja et al. 2001). The majority of natural products from cyanobacteria are lipopeptides, cyclic peptides and depsipeptides, and alkaloids (Moore 1996, Gerwick et al. 2001, Chorus 2001).

Cyanobacterial natural products can also serve as chemical defenses against grazers and competitors (Kirk and Gilbert 1992, Christoffersen 1996, Nagle and Paul 1999, Paul et al. 2001, Landsberg 2002). Freshwater cyanotoxins such as microcystins can have negative physiological effects (Fulton and Pearl 1987, DeMott et al. 1991, Rohrlack et al. 2001, 2005) and negative fitness consequences (Gustafsson et al. 2005) on zooplankton grazers such as *Daphnia* spp. Cyanobacteria can inhibit feeding by copepods (Fulton and Paerl 1987, Sellner et al. 1994). Although rapid increases in the abundance of cyanobacteria may be caused by factors similar to those that influence other algal blooms, such as nutrient enrichment, the interactive effects of eutrophication and herbivory on cyanobacterial populations are not well-understood (Thacker et al. 2001, Raikow et al. 2004).

Tsuda and Kami (1973) suggested that selective browsing by herbivorous fishes on macroalgae removed potential competitors and favored the establishment of unpalatable benthic cyanobacteria in tropical marine environments. Crude extracts and isolated secondary metabolites of several benthic marine cyanobacteria such as *Lyngbya* spp. have been tested in assays for feeding deterrence and are usually deterrent to generalist herbivores (Pennings et al. 1997, Nagle and Paul 1998, 1999, Capper et al. 2006). Thus, the chemical defenses of cyanobacteria may play a critical role in bloom formation and persistence by limiting the grazing activity of potential consumers.

UV tolerance

Many cyanobacteria are UV-tolerant and have evolved various mechanisms to counter UV radiation (Castenholz and Garcia-Pichel 2000, He and Häder 2002, He et al. 2002, Xue et al. 2005). For example, the UV-absorbing mycosporine-like amino acids (MAAs) are abundant in marine, freshwater, and terrestrial cyanobacteria (Garcia-Pichel and Castenholz 1993, Castenholz and Garcia-Pichel 2000, Liu et al. 2004). Shinorine, mycosporine-glycine, porphyra-334, and asterina 330 are among the MAAs identified in cyanobacteria (Figure 2). These colorless, low molecular weight, water soluble, UV-absorbing compounds are present under all growth conditions. They were found to increase in *Gleocapsa* when cells were exposed to UV radiation at 310-320 nm (Garcia-Pichel et al. 1993). Cyanobacteria also produce sheath pigments such as scytonemin, a yellow to brown-colored UV-absorbing pigment found in many different cyanobacteria (Figure 2). Exposure to UV radiation induces the production of scytonemin, which absorbs maximally at the longest wavelengths of the UV (approx. 380 nm) (Castenholz and Garcia-Pichel 2000). The UV-absorption of scytonemin complements the UV-absorption of the MAAs, which have absorption maxima ranging from 310 to 360 nm (Garcia-Pichel and Castenholz 1993). Other mechanisms of dealing with UV stress include antioxidant enzymes, such as superoxide dismutase, catalase, and glutathione peroxidase, and antioxidant molecules, including ascorbate, carotenoids, and tocopherols (Paerl et al. 1985, He and Häder 2002, Xue et al. 2005).

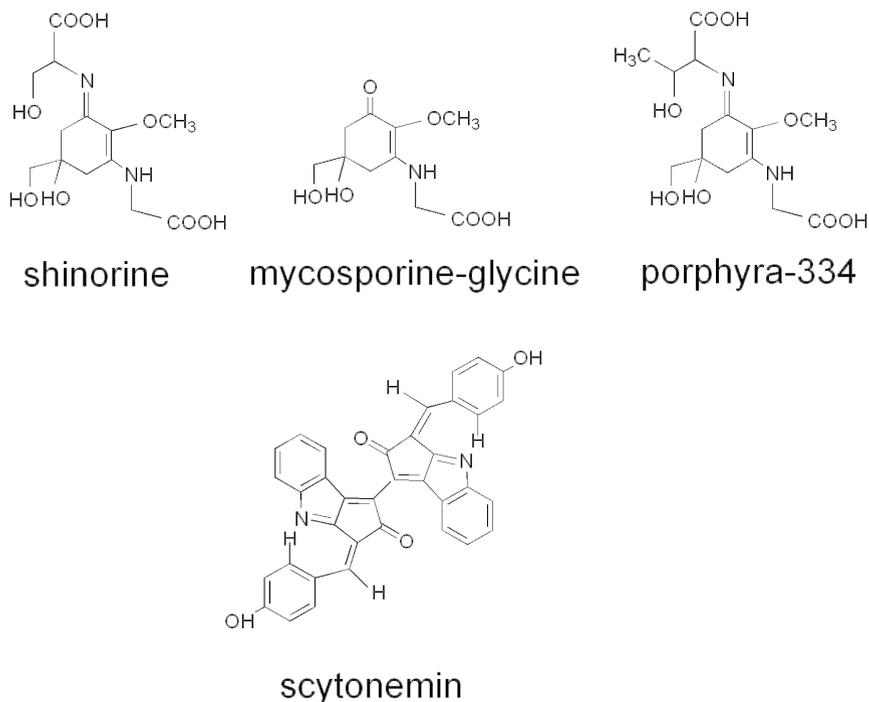


Fig. 2. MAAs (e.g. shinorine, mycosporine-glycine, porphyra-334) and the sheath pigment scytonemin are UV-absorbing compounds commonly found in cyanobacteria.

Temperature and light

Cyanobacteria often favor warm water temperatures and high light environments (Paerl et al. 1985, Robarts and Zohary 1987). In a study designed to understand the invasive behavior of the toxic, bloom forming cyanobacterium *Cylindrospermopsis raciborskii*, Briand et al. (2004) examined the growth of 10 strains of this cyanobacterium under different light intensities and temperatures. All 10 strains grew under a broad range of temperatures and light intensities, suggesting that the invasion of *C. raciborskii* into freshwater ecosystems at mid-latitudes may result from its ability to tolerate a variety of environmental conditions. Regional and global warming could provide this species with better environmental conditions for optimal growth, which occurs at temperatures approximately 30°C (Briand et al. 2004).

Trichodesmium species are globally significant, nitrogen-fixing marine cyanobacteria found throughout the tropical and subtropical oceans. *Trichodesmium* species inhabit low-nutrient, clear surface waters and are

adapted to a high light regime. Active growth occurs largely at temperatures above 20°C. Pigment composition and photosynthetic capabilities indicate maximum photosynthetic efficiency and effective photoprotection in high light environments (Capone et al. 1997). These cyanobacteria prefer warm water temperatures. For example, a bloom of *T. erythraeum* occurred in the Canary Islands Archipelago during August 2004, the warmest period recorded since 1912 (27.5°C) (Ramos et al. 2005). Blooms of *T. erythraeum* had not been previously recorded anywhere along the coast bordering the NW African upwelling zone, and this bloom event was thought to be associated with exceptionally warm weather and dust storms observed in the area (Ramos et al. 2005). Enhanced vertical stratification arising from increased warming of oceanic surface waters could also favor blooms of this buoyant genus.

Cyanobacteria have also been shown to be dominant in the warmer months in subtropical estuaries (Pensacola Bay, FL) (Murrell and Lores 2004). Cyanobacterial abundance (*Synechococcus*) peaked in the upper estuary during summer months. Their abundance at the freshwater end of the Bay was very low, suggesting they were not delivered to the estuary by freshwater. Changes in phytoplankton seemed to be related to changes in zooplankton composition, suggesting important trophic implications of a shift to cyanobacterial dominance.

Benthic marine cyanobacteria, such as *Lyngbya* species, have been documented to bloom in coastal environments with increasing frequency during the past decade (Paul et al. 2001, O'Neil and Dennison 2005, Paul et al. 2005). Large blooms of *Lyngbya majuscula* have been reoccurring seasonally in Moreton Bay, Australia, for several years. In an attempt to understand factors influencing bloom dynamics, Watkinson et al. (2005) assessed various environmental parameters before and during a bloom. A pulse of rainfall activity preceded the *Lyngbya* bloom they were monitoring, and a period of high incident light, water temperatures above 24°C, and calm weather conditions coincided with bloom initiation. The high temperature requirements for this cyanobacterium are similar to those reported for other cyanobacteria (Robarts and Zohary 1987). Nutrients (especially iron) carried by creeks flowing into the study region may have also contributed to bloom formation (Watkinson et al. 2005). Other studies have also documented the potential roles of phosphorus and iron in stimulating *Lyngbya majuscula* productivity and growth (Kuffner and Paul 2001, Elmetri and Bell 2004, Albert et al. 2005).

The black band disease cyanobacterium *Phormidium corallyticum*, a major component of the microbial consortium that causes this common coral disease, photosynthesizes maximally under aerobic conditions at water temperatures of 30-37°C (Richardson and Kuta 2003). Field observa-

tions report that black band disease is most common during the summer months, and these data suggest that water temperature is one of the most important factors in the seasonality of black band disease (Richardson and Kuta 2003). Elevated water temperatures $>30^{\circ}\text{C}$ can cause bleaching and mortality among many coral species (Donner et al. 2005); impaired coral physiology might also contribute to black band disease occurrence.

Light and temperature influence growth rates as well as toxin production for many species of cyanobacteria (Sivonen 1990, Rapala et al. 1997). Several studies have shown that toxin production in *Microcystis aeruginosa* increases with irradiance under light-limited conditions (Watanabe and Oishi 1985, Utkilen and Gjolme 1992, Weidner et al. 2003). Microcystin composition of *Planktothrix agardhii* changed toward a higher proportion of a more toxic variant with increased light intensity (Tonk et al. 2005). Pangilinan (2000) found that light levels influenced growth and production of the compound pitipeptolide A by *Lyngbya majuscula*. The cyanobacterium grew twice as much and contained significantly more pitipeptolide A at higher light levels of $135\text{--}169\ \mu\text{mol photon m}^{-2}\ \text{s}^{-1}$ than at light levels approximately half that amount after four weeks. Temperature is also an important factor affecting both growth and secondary metabolite accumulation in cyanobacteria (Watanabe and Oishi 1985, Sivonen 1990, Rapala et al. 1997, Lehtimaki et al. 1994). In recent years, understanding of the genetics of cyanotoxin biosynthesis has advanced considerably (Tillett et al. 2000, Dittmann et al. 2001, Kaebernick et al. 2002, Edwards and Gerwick 2004). This facilitates molecular approaches to studying how light and other environmental factors may influence cyanotoxin production (Kaebernick et al. 2000, Kaebernick and Neilan 2001).

Temperature, light, and nutrients may have interactive effects on growth and toxin production, with consequent effects on aquatic food webs. One laboratory study showed that increases in water temperature could increase the susceptibility of rotifers to toxic effects of anatoxin-a produced by *Anabaena flos-aquae* (Gilbert 1996). Moss et al. (2003) studied the effects of warming, nutrient addition, and fish on phytoplankton composition in mesocosms designed to mimic macrophyte-dominated shallow lake environments. Warming 3°C above ambient had smaller effects on the phytoplankton community than did the presence or absence of fish (sticklebacks, *Gasterosteus aculeatus*) or addition of nutrients. Contrary to expectation, warming did not increase the abundance of cyanobacteria in the experimental treatments.

Nutrients- rainfall patterns

The amounts and chemical composition of nutrients sources (especially N and P) to freshwater and nearshore coastal waters are well known to influence cyanobacterial bloom formation and dynamics. This topic has been reviewed elsewhere in these proceedings (Pearl 2006). Some climatic effects of global change, including variation in rainfall patterns (Walther et al. 2002, Treydte et al. 2006), floods, droughts, dust storms (Prospero and Lamb 2003), tropical storms, and intensity of hurricanes (Webster et al. 2005) can synergistically (along with nutrients) impact cyanobacterial and algal communities and bloom dynamics. The consequences of these changing patterns, their impact on nutrient entry and utilization in the freshwater-marine continuum (Carpenter et al. 1992), and the interactions between nutrients and other environmental factors on cyanobacterial bloom formation and cyanotoxin production have largely not been investigated.

Ecological and ecosystem consequences

Few specific examples address the ecological consequences of global warming on cyanobacterial blooms and their dominance in aquatic ecosystems. Variable results have been obtained from the few studies that address this topic (Moss et al. 2003, Briand et al. 2004, Ramos et al. 2005).

Cyanobacterial abundance can increase during warmer years, suggesting that global warming will have long term effects on phytoplankton communities. A 42-year record of primary productivity in a small, subalpine lake (Castle Lake, northern California) showed that *Daphnia* and cyanobacterial biomass were higher during warmer years (Park et al. 2004). Increasing water temperatures were accompanied by increasing summer cyanobacterial biovolume, whereas other phytoplankton groups did not show significant trends with water temperature. The authors suggested that changes in air temperature and precipitation as a result of global warming, the Pacific Decadal Oscillation, and El Niño Southern Oscillation could influence primary productivity and plankton communities in North American dimictic lakes (Park et al. 2004). Other studies have also shown correlations between climate variation, often related to the North Atlantic Oscillation (NAO), and spring plankton dynamics and clear water phases in shallow, polymictic European lakes (Gerten and Adrian 2000, Scheffer et al. 2001). Cyanobacteria can be abundant in polymictic shallow lakes, with rapid and intense blooms reported in spring and summer (Abrantes et al. 2006).

Lake Tanganyika, a large rift valley lake in east Africa, has been surveyed and records of its nutrients and temperatures have been published several times in the past century. Temperatures have increased in the past century by 0.9°C at 100 m, with 50% of the heat gained by the lake in the upper 330 m. The lake records show a century-long warming trend, and impacts on its planktonic ecosystem are reported (Verburg et al. 2003). A sharpened density gradient, a consequence of surface warming, has slowed vertical mixing and reduced primary production. The phytoplankton biomass in 2000 was lower than in 1975 by 70%, and the composition of the phytoplankton also changed. Cyanobacteria comprised a larger portion of the total biomass in March to April 2001 than they did during the same time in 1975 (Verburg et al. 2003).

Conclusions

Examination of the evolutionary history of cyanobacteria, studies of their ecophysiology, and recent investigations of phytoplankton dynamics and community structure in response to global climate change all suggest that cyanobacteria will probably thrive under environmental conditions associated with global warming. Most studies addressing cyanobacterial responses to changes in irradiance, temperature, and nutrients have been done in the laboratory; few studies have addressed these important topics under field conditions. Clearly, studies of changes in cyanobacterial community composition, bloom dynamics, and toxicity in response to increasing temperatures and other environmental factors associated with global warming are of great importance to our understanding of harmful cyanobacterial bloom dynamics. Interactions among anthropogenic effects, including eutrophication and food web alterations, and changing environmental conditions are likely to be complex. A much better understanding of these issues is urgently needed.

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